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The Nasal Capsule Of Amphibia

UNIVERSITY OF ILLINOIS
THE NASAL CAPSULE OF AMPHIBIA

BY

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B. S. Knox College, 1914

THE NASAL CAPSULE OF AMPHIBIA
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I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY SUPER-
VISION BY George Marsh Higgins

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DEGREE OF Master of Arts.

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I. INTRODUCTION.

The work upon the cartilaginous nasal capsules of several Urodele Amphibians here described, is the beginning of an investigation upon the nasal organs of the lower tetrapodous vertebrates. It is the hope that when these investigations are completed that they may throw some light upon the inter-relationships and classification of the several orders of the Amphibia and the lower reptiles.

The work has been done in the laboratory of Prof. J. S. Kingsley, entirely with wax models after the Born method and is largely based upon the University material.

There already exists a considerable literature upon the chondrocranium of the Amphibia, though there is far less relating to the detailed study and morphology of the nasal capsules. The articles which have been of use to me in the preparation of this paper are quoted in the accompanying bibliography, but any discussion of the results of previous work is hardly advisable until the entire Amphibian nasal capsule can be considered.

I desire to thank Prof. Kingsley for his kind criticism and many helpful suggestions during my study and the preparation of this paper.

II. DESCRIPTION.

Amblystoma was selected as the basis of these studies because of the larger number of stages of material available and of its median position among the Urodeles.

In an embryo of 11 mm. body length, chondrification has advanced but little and few features of a nasal capsule can be seen. Just anterior to the eye the trabeculae bend toward each other, but do not meet in the middle line. At its distal end, each trabecula expands into a flat horizontal plate, which contains the elements of the ethmoid and the cornu trabeculae. At this stage, on one side only, were a few cartilage cells a little above and medial to the median margin of the ethmoidal region. These cells are the first appearance of a couple of longitudinal cartilage bars, the columnae ethmoidalis, which are well-developed in the next stage to be described.

In a larva 20 mm. long, chondrification is much more advanced. In the nasal region, the trabecular expansions have fused in the median line, forming the ethmoid plate which is slightly excavate dorsally for the anterior end of the telencephalon. It is limited dorsally on either side by a marked thickening, the extension forward and slightly inward of the trabeculae. Between these lateral boundaries the ethmoid plate is about twice as broad as long. Its posterior margin is slightly arcuate and passes laterally into the trabeculae; the anterior is more nearly a straight line, limited on either side by the inner margins of the cornua trabeculae.

Each cornu trabeculae projects laterally and forward from the anterior end of the trabecular thickening in approximately the same plane as the ethmoid plate. The posterior limit of the base of either cornu is about on the level with the mid-

dle of the ethmoid plate; from this point its posterior margin extends forwards and outwards, then bends sharply outward and backwards to the posterior-external angle of the cornu. The antero-lateral margin of the cornu is at about an angle of 45 degrees to the median axis of the skull and meets the inner margin of the cornu, extending forward from the anterior margin of the ethmoid plate, at an acute angle.

Dorsal and parallel to the trabecular extension of either side is an elongate rod of cartilage, separated from the parts described above by not more than its diameter. This is the columna ethmoidalis and is the later development of the dorsal anlage mentioned in connexion with the 11mm. stage. It is of especial interest to note that this rod, though later fusing with the trabecula arises independently of it. The olfactory nerve passes between this rod and the trabecular extension.

Terry has described ('06) an antorbital process as occurring in a 12 mm. larva. My sections do not show any indication of this process in the 20 mm. stage.

In a larva 34 mm. long, many additional features have been added to the nasal capsule. The columnae ethmoidalis have now completely fused with the trabeculae to form the anterior part of the lateral walls of the cranial cavity. On the dorsal side, the anterior part of the ethmoid columns have fused with the ethmoid plate and posteriorly they have united with the dorsal crests of the trabeculae; so that column and crista of either side appear as one continuous elevation, with the olfactory foramina passing through it. Just in front of these foramina the ethmoid plate, which is thin behind, becomes abruptly thickened between the anterior ends of the columns and this thickening,

which forms the broad nasal septum, extends anteriorly and laterally on the medial margins of the cornu trabeculae. By reason of these antero-lateral expansions of the septum, the anterior margin of this planum ethmoidalis and the septum becomes deeply excavate, a condition which persists in later stages. Anterior to the olfactory foramen each ethmoidal column has expanded laterally from its dorsal surface to form the median nasal process, a covering for the mesal margin of the nasal sac. Each lateral expansion is continued toward the anterior end and near its cephalic limit is perforated by a small opening, the foramen of the ramus externus branch of the V nerve.

The lateral cephalic expansions of the ethmoid plate are the cornua trabeculae. These plates are roughly triangular in outline and are slightly concave dorsally to support the cephalic portion of the nasal organ. The lateral margin is broadly convex, embracing an arc of almost 90 degrees, as it curves laterally and ventrally from the emarginate limits of the ethmoid plate to a point in a line with the caudal limits of the septum. From its junction with the lateral margin, the posterior margin is directed mesad for a short distance when it turns abruptly cephalad and then with a broad sweeping curve it is continued posteriorly and fuses with the caudal lateral margin of the ethmoid plate ventral to the olfactory foramen.

At a point just dorsal to the olfactory foramen a strong lamina cribosa extends laterally and anteriorly, and curves slightly downward over the olfactory organ. Approximately dorsal to the gap between the antorbital process and the cornu, the lateral margin of the lamina cribosa descends nearly to the level of the gap between them. The posterior margin of the lam-

ina is oblique; its lateral margin slightly arcuate, while in front it continues forward as a small conical process to a position in line with the anterior margin of the gap between the cornu and the antorbital process, and is limited on its mesal margin from the septum nasi by a deep notch, the narina fenestra. The material of *Amblystoma* was not sufficient to determine the question of how the lamina cribosa arises, but a reconstruction of this region in *Salamandra atra*, to be described later, shows that at least in that species the cribosa is developed as a lateral outgrowth from the columna ethmoidalis.

Antorbital processes are now present, and are formed from the ventro-lateral angles of each trabecula. Their anterior margin is in line with the posterior limit of the ethmoid plate and their length is about equal to the height of the trabecula in this region. These processes extend laterally a distance equal to their length and then bend abruptly forward and terminate anteriorly in a small projection posterior to the caudal lateral angle of the cribosa. I have no evidence in my material as to the origin of the antorbital processes, but according to Terry, these cartilages arise as separate chondrifications and later fuse with the trabeculae.

The nasal capsule at this stage is far from completion. The olfactory organs lie lateral and anterior to the brain and are contained in a cavity lateral to the trabecula and septum. The capsule is composed of a median lateral wall, a roof and a floor. This median wall is formed by the columna ethmoidalis and a part of the septum, while posterior to the olfactory foramen it is formed by the crista trabecula. Near the anterior end of the columna part of the wall is a small foramen through which

the ramus externus branch of the V nerve passes from the capsule to the dorsal surface of the tip of the snout. The anterior part of the nasal cavity is arched over by a lateral extension of the ethmoidal column and the median nasal process, which extends back to the lamina cribosa, beyond which there is no such similar extension of the trabecular crest. The floor of the capsule is composed of the cornu and the antorbital process, which are separated by a large gap. The lamina cribosa functions as a roof for the caudal portion of the nasal sac, and bends downward and laterally so that its lateral margin extends to a line joining the lateral margins of cornu and antorbital process.

In a 45 mm. larva, chondrification has not greatly advanced beyond the condition as described for the 34 mm. stage. The nasal capsule has not increased in length, but there is a small increase in width. The striking contrast between the capsules of these two stages rests in the increased bulk and thickness of the 45 mm. capsule. With the increased size of the olfactory lobes, there is a corresponding increase in that of the anterior part of the brain case which now is approximately hemispherical. The nasal septum has decreased slightly in length as well as in width, though it is twice as thick as in the 34 mm. stage. Its posterior dorsal margin is broadly concave, while its posterior surface is almost vertical to the plane of the ethmoid plate which curves downward and backward. The intra-trabecular notch, bounding the septum in front is arcuate; its lateral portions passing by a broad curve into the anterior medial sides of the cornu.

The capsule presents the same elements as described for the 34mm. stage. The medial nasal processes of the ethmoidal col-

umns have increased in width and now form a roof for the mesal half of the nasal organ. The foramen of the ramus externus nerve is in the approximate middle of each nasal process. The olfactory foramina have increased in size and are directed more laterally than antero-laterally as was true for the 34 mm. stage.

The lamina cribosa has increased in size and has fused by its anterior distal angle with the posterior lateral process of the trabecula, so that now a complete band of cartilage is formed around the external nares. The resulting nasal canal is an elongate ovoid, or some-what almondshaped. On its dorsal aspect it is exposed by the broad fenestra narina, on its ventral aspect by the wide gap between the cornu and the antorbital process, which are now present though on a somewhat smaller scale than in the 34 mm. stage. Winslow has shown that in stages older than any that I have studied that these processes unite to the posterior margin of the cribosa.

SALAMANDRA ATRA.

In a larva of *Salamandra atra*, 25 mm. long, chondrification has so far advanced that the nasal capsule is distinctly outlined to an extent intermediate between the 20 mm. and the 34 mm. *Amblystoma* larvae, and may afford an explanation of some of the changes in the older *Amblystoma* stages.

The trabeculae extend forward to the level of the caudal limits of the nasal organ; then they turn abruptly mesad to unite to form the broad ethmoid plate. This plate is trapezoidal in outline, its posterior margin being parallel to and a half longer than the anterior margin. Laterally, the ethmoid plate is bounded dorsally by the same elevated lines - the extensions of the trabeculae - noted and described in *Amblystoma*.

Dorsally the ethmoid plate is broadly concave to receive the olfactory lobes, the ventral surface being parallel to the dorsal. The anterior margin is straight between the cornua, but the posterior bears a strong triangular process which is lacking in the later stages and in all stages of all other Urodeles studied.

Anterior to the ethmoid plate the trabecular swellings disappear, while on either side is the broad plate of the cornu. These are thin, slightly curved, triangular plates which support the cephalic portion of the nasal organ. Their antero-lateral margins are distinctly curved in a latero-posterior direction, and terminate in the lateral angle at the level of the anterior limits of the ethmoid plate. The posterior margin of each cornu is directed mesad, perpendicular to the main axis for about one-half the width of the cornu, then it turns obliquely posterior and fuses with the trabecula upon its lateral aspect.

Parallel to each trabecular swelling and separated from them by a distance equal to twice its width, is the columna ethmoidalis, which has fused anteriorly with the dorsal surface of the anterior part of the cornu trabeculae, a condition apparently intermediate between the 20mm. and the 34mm. stages of *Amblystoma*. Each column extends upwards, outwards and backwards to the level of the caudal margin of the ethmoid plate, where it bends sharply laterad and arches downward above the caudal portion of the olfactory organ. This is the anlage of the lamina cribrosa described in the 34 mm. *Amblystoma* larva and apparently explains the origin of this structure.

Antorbital processes are given off from the lateral angles of each trabecula, and are directed latero-ventrally and then turn abruptly anteriorly for a distance equal to the length

of the process and terminate at the level of the caudal margin of the ethmoid plate.

In a *Salamandra* larva 38 mm. long, the nasal capsules shows resemblances to that of the 45 mm. *Amblystoma*. At this stage chondrification has advanced in all parts, thus effecting a much more complete protection for the olfactory organs. The *cristae trabecula* which were just beginning to chondrify in the 25 mm. stage have now completely formed and have united in front with the caudal limit of the *columnae ethmoidalis*, thus forming the lateral walls of the brain case in this region.

The ethmoid plate, though still trapezoidal in outline, has completely lost the process from its posterior margin described in the earlier stage; so that now this margin is semicircularly excavate like the posterior margin of the ethmoid plate of the 45 mm. *Amblystoma* larva. The lateral swellings of the *trabeculae* still persist, giving the plate its characteristic excavate dorsal surface.

Anterior to the ethmoid plate and located between the nasal organs is a small nasal septum, formed by a fusion in the middle line of the cephalic ends of the *columnae ethmoidalis*. This septum is very small, its dorsal surface being equal in length to about one-seventh of that of the entire capsule. In the middle line there is a gap, the *fenestra naso-basalis*, between this nasal septum and the ethmoid plate, through which the *ramus medialis* nerve passes to the well-known intermaxillary gland, which lies in the intra-trabecular notch just in front of the septum. The bar of the septum which closes the *fenestra* above is triangular in sagittal section; its posterior side being vertical, the dorsal surface flat and the anterior face extending downwards

and backwards meets the ventral posterior margin at an angle of about 60 degrees.

Anterior to the olfactory lobes the united columna ethmoidalis and cornu extend forward a distance about equal to the length of the septum nasi. The median nasal process has extended laterally from the dorsal margin of each column to form a roof for the cephalic portion of the olfactory sac, while posteriorly it unites to the lamina cribosa yet to be described. At the anterior end there has been a similar lateral growth from the crista, closing in the capsule in front so that the nares forms an elongate gap, opening obliquely outwards and forwards. Upon the mesal surface of this cartilage cap, just anterior to the septum is the small foramen for the ramus externus branch of the V nerve.

The lamina cribosa, which arose as a lateral process from the caudal limit of the ethmoidal column, has increased in size, growing laterally and ventrally over the posterior portion of the nasal sac, uniting with its ventral anterior angle to the caudal margin of the cornu and thus forms a complete band of cartilage around the middle portion of the olfactory organ, much as described in the 45 mm. *Amblystoma*.

The cornu trabeculae, which forms the floor of the capsule is distinctly convex on its ventral aspect and extends laterally as far as the roof of the capsule. At the anterior end of the ventral surface of each cornu a small cartilage, the prenasal process is given off. At this stage the olfactory foramina have not completely formed, but the olfactory nerve passes through a large fenestra extending from the anterior level of the ethmoid plate almost to the line of its posterior margin, between the columna ethmoidalis and the trabecular extensions of the ethmoid plate.

Extending from the ventral lateral margin of each trabecula is the antorbital process. It is more slender than that of *Amblystoma*, and extends laterally a distance equal to the height of the trabecula and then extends cephalad a distance equal to its length.

The 38 mm. *Salamandra* is somewhat in advance of that stage described for the 45mm. *Amblystoma*. Except for the incomplete formation of the olfactory foramina the nasal cavity of each side is more completely closed. The lateral extension of the medial nasal process and its fusion to the lamina cribosa effects a complete covering for the entire dorsal aspect of the nasal sac. The floor of the capsule is formed by the expanded cornu trabeculae on its anterior half and by the antorbital process posteriorly. The lateral aspect of each nasal sac is uncovered by the oblong fenestra between the lateral margins of cornu and nasal process, the fenestra narina. In striking contrast to the open anterior end of the capsule in *Amblystoma* is the completely closed end in *Salamandra*, a change made necessary by the shifting of the external nares from a terminal to a lateral position.

TRITON CRISTATUS.

The nasal capsule of *Triton cristatus*, though bearing some resemblances to *Salamandra* and *Amblystoma* shows many striking contrasts. In a larva 28 mm. long, the capsule is somewhat rectangular in outline, the width slightly exceeding its length at its widest part, and gradually tapering toward its anterior end. At this stage the cristae trabeculae are well developed, being wider at their ventral than at their dorsal margins, and, extending in a latero-dorsal oblique direction, they form the

lateral walls of the brain case in this region. Slightly anterior to the antorbital processes, the trabeculae fuse on their ventral margins to form a very small ethmoid plate. This plate, strikingly in contrast to the broad ethmoid plate of both *Amblystoma* and *Salamandra*, is equal in length to about half the width of the olfactory foramen and connects the trabeculae of either side at a point just posterior to the anterior margin of the foramen. It is roughly trapezoidal in outline, as in *Salamandra*, its anterior margin being parallel to, but about three-quarters as long as the posterior margin.

Dorsal to and separated from the planum ethmoidalis by a considerable distance, is a narrow cartilaginous bar, the nasal septum. This septum unites the capsules of either side upon their dorsal aspect at a point just anterior to the cephalic margin of the olfactory foramen and is separated from the ethmoid plate by a large naso-basalis fenestra, which conducts the ramus medialis nerve to the inter-maxillary gland.

In contrast to the conditions in both *Salamandra* and *Amblystoma*, the nasal organs of *Triton* are entirely cephalad to the brain. As a result the greater part of the nasal capsule lies anterior to the nasal septum and appears as a segment of an elongate cone, obliquely truncated anteriorly, and with its lateral wall interrupted by the very large narial opening. The strongly convex medial walls of the two capsules are nearly parallel to each other, the cavum intermaxillare between them being about three times as long as broad. On the lateral and dorsal surface of each capsule, near the dorsal boundary of the external naris is a large oblique oval fenestra, the bar separating it from the lateral margin forms a connexion between the dorsal

lateral expansion of the columna ethmoidalis with the lamina cribosa.

The lamina cribosa forms a vault, extending from the septum nasi to the anterior end of the trabecular crest, and laterally to form the widest part of the capsule, its posterior margin being nearly a straight line at right angles to the major axis of the skull. This hinder margin arises proximally from the dorsal portion of the crista trabecula and extends outwards and downwards so that its distal angle is about on the level with the ethmoid plate. In the lateral view the ventral margin of the lamina cribosa is irregular, a gap existing between it and the floor of the capsule which extends forward to a slender bar of cartilage which connects the anterior portion of the lamina cribosa with the posterior margin of the floor, similar to that described in *Amblystoma*.

In the ventral aspect of the capsule, the trabecular extensions have expanded into a trapezoidal cornu which forms the floor of the capsule and is uninterrupted as far back as the level of the septum nasi; from this point posteriorly the inner wall of the capsule is formed by the expanded basal portion of the trabecula. At the anterior end the floors of the two capsules approach each other, and at the extreme medial ventral tip of each is a short cartilaginous projection possibly the homologue of the prenasal cartilage of *Salamandra*. Just above and lateral to these processes are the foramina for the ramus externus branch of the V nerve. The antorbital processes extend laterally from the ventral margin of the crista trabecula just posterior to the caudal limits of the ethmoid plate, their length being about equal to the height of the trabecula in this region.

In an older *Amphiума means* larva, the nasal capsule has been completely chondrified and represents a condition similar in some respects to *Amblystoma*. It is somewhat ovoid, its greatest width being about two-thirds its length; both crista and trabecula have formed and these have united to form the lateral wall of the brain case in the region of the eye. Just anterior to the optic region the trabeculae become distinct and are directed toward the anterior and slightly mesad; they continue cephalad for a distance equal to half the length of the capsule. Their fusion at this point forms the ethmoid plate, which supports the mesal portion of the anterior part of the olfactory organs. This plate is roughly six-sided. The posterior margin is straight and at right angles to the middle line of the skull, while each lateral caudal margin is distinctly curved and is marked by a line directed latero-anteriorly to a point where it fuses to another cartilage to be described later. Each lateral cephalic margin is also curved and is marked by a line directed anteriorly to a point where it passes into the anterior margin which is strongly arcuate, thus giving a forked appearance to the anterior portion of the plate. Thus the planum ethmoidalis is united upon its posterior margin to the trabeculae, on each lateral aspect to a cartilage bar yet to be described, and on its anterior margin, it is continued as a pair of small expanded processes, the cornu trabeculae.

From the median dorsal aspect of the planum ethmoidalis, just posterior to the deep intra-trabecular notch, the short nasal septum extends dorsally a distance equal to the width of the ethmoid plate at its posterior margin. Upon its dorsal mar-

gin the septum divided into two cartilages which are directed from the line of the septum at an angle of about thirty degrees. Continuing dorso-laterally for a short distance each cartilage unites upon its caudal margin to the tectal cartilage, while each cephalic margin continues cephalad a short distance and ends at a line just posterior to the plane marking the anterior limits of the trabecular extensions.

From the dorsal anterior margin of each crista, dorsal and lateral to the trabecula, a small cartilage bar, the columna ethmoidalis, is directed anteriorly and slightly bends out over the dorso-lateral aspect of the nasal organ. It continues anteriorly about a third the length of the capsule and then divides into two bars, one of which turns abruptly mesad and becomes the tectal cartilage and extends obliquely over the median dorsal aspect of the nasal sac to unite with the caudal half of the septum nasi. The other division of the crista trabecula becomes distinctly broader to form the lamina cribosa, the only lateral covering of the olfactory sac in this region. A slender rod equal in width to the tectal cartilage, continues forward from the anterior ventral margin of the cribosa to the plane of the posterior limit of the nasal septum, where it abruptly doubles in width and at the same time gives rise to a small cartilaginous process which continues ventrally and slightly mesad to unite with the lateral extensions of the ethmoid plate. The broad band of cartilage resulting from the fusion of these cartilages extends anteriorly and, at its distal end, expands into a ring of cartilage which entirely surrounds the nasal duct where it passes to the exterior. Antorbital processes are present as small short rods extending in an anterior lateral direction from the ventral cephalic

margin of the crista trabecula.

In some respects the nasal capsule of *Amphiuma* represents a stage intermediate between *Necturus* and *Amblystoma*. The openness of the capsule and the consequent exposure of the nasal organs is similar to the condition to be described for *Necturus*, yet the ethmoid plate, nasal septum, trabecula and the tectal cartilages can all be homologized with conditions described for *Amblystoma*. The separation between the nasal organs is only slight because of the reduced size of the septum. The anterior lobes of the brain extend forward to the septum and the olfactory sacs lie adjacent to it upon either side separated from it by membrane only. The olfactory nerve passes beneath the tectal cartilage to unite to the olfactory lobe. Dorsally each nasal cavity is bounded by a tectal cartilage only; ventrally the cornu trabeculae and the antorbital process comprise the floor, while laterally the lamina cribosa and its anteriorly directed cartilage only partially cover this aspect of the nasal organ.

NECTURUS MACULATUS.

In a 45 mm. *Necturus* larva, the nasal capsule bears some striking contrasts to either of the *Urodeles* above described. It is rectangular in outline, gradually tapering from its greatest width, the region of the antorbital processes, to the anterior end. Just anterior to the eye the trabeculae are oval in cross section and are widely separated from each other, though slightly directed toward the middle line. By the fusion of these trabeculae in the middle line at the median region of the nasal capsule, a broad ethmoid plate is formed; trapezoidal in outline, its posterior margin being parallel to and three times the length of the anterior margin, while its length is equal to its greatest

width. The swellings of the trabecular extensions are conspicuous on the caudal lateral margins of the plate, thus giving the dorsal surface the characteristic excavate outline to receive the anterior lobes of the brain; while upon the cephalic lateral margins these swellings are not prominent and the median region of the anterior half is distinctly elevated into a prominent ridge which extends to the cephalic margin of the septum. This slight ridge is the only indication that the capsule presents of a nasal septum, which is a more completely developed organ in the other Urodeles. Continuing anteriorly from the cephalic margin of the planum ethmoidalis are the cephalic extensions of the trabeculae. These extensions are thin plates, equal in length to about three-fourths of that of the ethmoid plate and equal in width to the diameter of the trabecula posterior to the ethmoid plate. Their anterior margins mark the cephalic limits of the nasal organs.

In contrast to *Amblystoma* and its near relatives the roof of the nasal organ of *Necturus* is entirely distinct from that part of the capsule described above. Dorsal and lateral to the trabeculae and the trabecular extensions, and separated from them a distance equal to the width of the extension, are a pair of cartilaginous rods, the columnae ethmoidales, which extend in a postero-oblique direction from the cephalic limit of the capsule to a position just anterior to the antorbital processes. From their lateral margins fenestrated cartilaginous processes extend laterad and ventrad around the olfactory organ, forming the well-known lattice work capsule. Chondrification of these processes is more advanced in the posterior region, the caudal portion of the olfactory organ being more completely covered than is the cephalic, since the lateral outgrowths of the columna ethmoid-

alis have not yet appeared on its anterior third. It is of interest to note that this ethmoidal column chondrifies separately, as is also true of the column as described for *Amblystoma*, but that in contrast to *Amblystoma* it does not later fuse to the trabecula but remains distinct from it throughout life.

Olfactory foramina are not as yet formed. The olfactory nerve passes between the columna ethmoidalis and the trabecula at a point just posterior to the ethmoid plate and enters the olfactory lobe near its anterior end, which rests upon the caudal portion of this plate. Antorbital processes extend from the ventro-lateral margins of the trabeculae laterad for a short distance and then obliquely cephalad to a point just posterior to the caudal limit of the fenestrated processes of the column.

The general openness of this capsule is in contrast to the closed capsule of the 38 mm. *Salamandra* and the 45 mm. *Amblystoma* larvae. The olfactory organs are exposed on their mesal, lateral and ventral aspects and are partly enclosed upon their dorsal aspect. The cornu trabecula, crista and lamina cribosa are not developed; and these features, together with the vestigial septum as well as the openness of the capsule all suggest an ancestral, degenerate or neotenic condition.

III. SUMMARY.

From the preceding description of the various Urodelan nasal capsules, there are several important characteristics to be enumerated. In all the members of this order, the capsules are built upon the same general plan, the modifications arising in connexion with the accessory structures. Trabeculae, which vary in shape from the oval rods of *Necturus* to well-developed cristae

of *Amblystoma*, are present in all forms studied. The direction of these trabeculae toward the middle line and their subsequent fusion to form the ethmoid plate is the one striking similarity between all these nasal capsules; though variations in size do occur, from the broad ethmoid plate of *Necturus* to the very small one of *Triton*, yet in all the larvae, the anterior portion of the telencephalon rests upon it. The nasal septum, conspicuous for its size and function in *Amblystoma* where it effects the only separation between the nasal organs, has become very much reduced in *Triton*, while in *Necturus* its only remnant is to be found in a slight elevation upon the anterior portion of the dorsal surface of the ethmoid plate. All larval forms develop an ethmoidal column which chondrifies independently, and secondarily, in *Amblystoma*, *Salamandra* and *Triton* becomes fused to the crista and the ethmoid plate; while in *Necturus* this column does not fuse with but remains distinct from the ethmoid plate throughout life. *Amphiuma* presents a condition somewhat intermediate in which the columna ethmoidalis has united posteriorly to the crista and anteriorly upon its ventral aspect to the ethmoid plate; but the absence of a strong lamina cribrosa and a wide medial nasal process differentiates it strongly from the *Amblystomal* capsule.

An interesting comparison is to be seen in the spatial relations between the olfactory organs and the brain. This series of capsules ranges in the relation of these organs from the condition in *Necturus* where the brain is adjacent to the caudal two-thirds of the nasal organ and separated from it by membrane only, through *Amphiuma*, *Amblystoma*, *Salamandra* and to *Triton* where we find almost the entire nasal sacs are located anterior

to the brain and are separated from each other by a pair of cartilaginous walls. This condition observed for Triton is suggestive of the Anuran capsule which I hope to consider at a later time, in which the olfactory organs are entirely cephalad to the brain.

Upon the basis of capsule differentiation and specialization Necturus is the more primitive. Related to this and yet more specialized in parts, indicating a relation to the higher Urodeles is Amphiuma; and finally Amblystoma, Salamandra and Triton, on the basis of capsule differentiation alone, stand the highest in this Urodelan order of Amphibia.

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V: ABBREVIATIONS USED.

- a. p., antorbital process.
- c. e., columna ethmoidalis.
- c. i., cavum intermaxillare.
- c. t., cornu trabecula.
- cr.t., crista trabecula.
- d. l. f., dorso-lateral fenestra.
- e. p., ethmoid plate.
- ex. n., external nares.
- f. n., fenestra narina.
- f. nb., fenestra naso-basalis.
- f. r. e., foramen of ramus externus branch of V nerve.
- fen. pr., fenestrated process.
- i. t. n., intra-trabecular notch.
- l. c., lamina cribosa.
- m. n. p., medial nasal process.
- n. s., nasal septum.
- o. fen., olfactory fenestra.
- o. f., olfactory foramen.
- p. c., prenasal cartilage.
- p. t. p., posterior triangular process.
- t., trabecula.
- t. e., trabecular expansions.
- t. s., trabecular swellings.

VI EXPLANATION OF PLATES.

Fig. 1,-----*Amblystoma punctatum*, 11 mm. long.

- | | | | | | |
|---|----------|---|---|------|-------------------|
| " | 2,----- | " | " | 20 " | " |
| " | 3,----- | " | " | 34 " | " , dorsal view. |
| " | 4,----- | " | " | 34 " | " , ventral view. |
| " | 5,----- | " | " | 45 " | " , dorsal view. |
| " | 6,----- | " | " | 45 " | " , ventral view. |
| " | 7,----- | <i>Salamandra atra</i> , 25 mm. long, dorsal view. | | | |
| " | 8,----- | " | " | 38 " | " , " " |
| " | 9,----- | <i>Triton cristatus</i> , 28 " " , " " | | | |
| " | 10,----- | <i>Amphiuma means</i> , older, ventral view. | | | |
| " | 11,----- | <i>Necturus maculatus</i> , 45 mm. long, dorsal view. | | | |

PLATE I

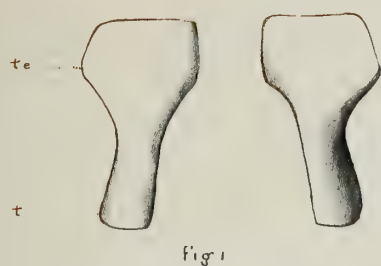


Fig 1

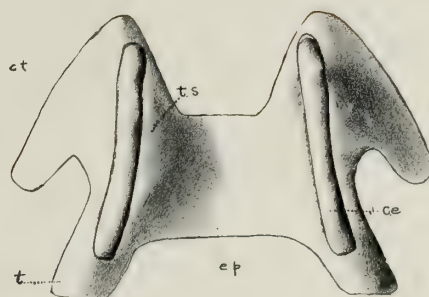


Fig 2

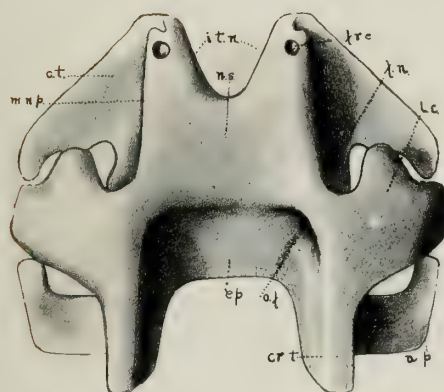


Fig 3

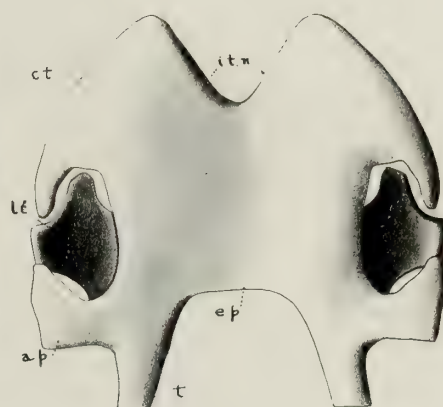


Fig 4

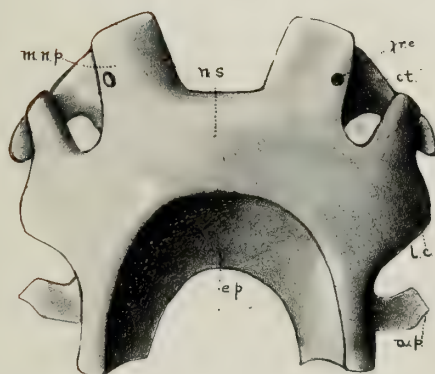


Fig 5

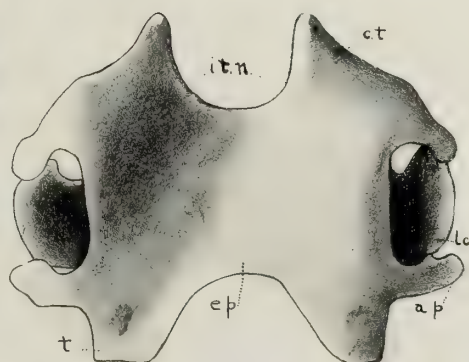


Fig 6

PLATE II

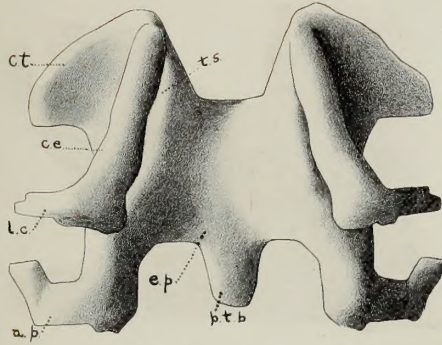


Fig. 7

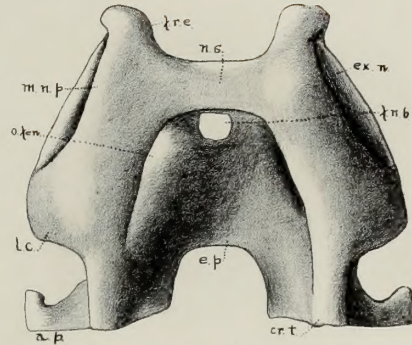


Fig. 8

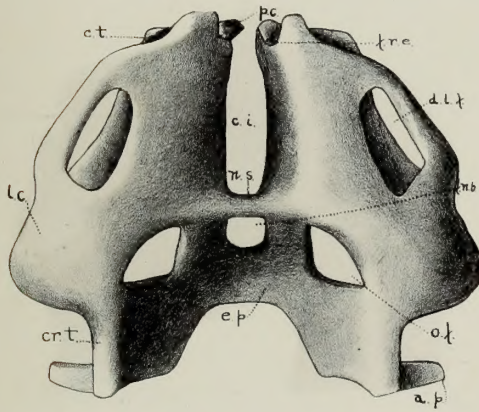


Fig. 9

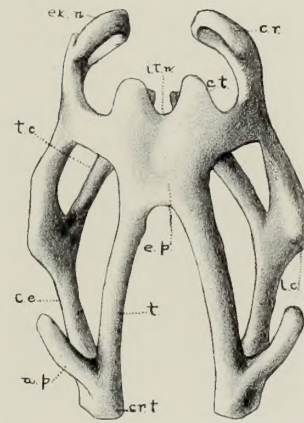


Fig. 10

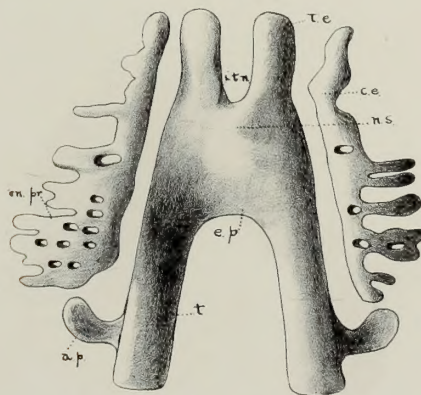


Fig. 11

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